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Abstract

The oral cavity is the place where the food is manipulated and disrupted by teeth during mastication to form a food bolus ready for swallowing. The human masticatory system is an integrated functional unit with a highly complex organization, and its functioning depends on a set of organs and tissues whose activities are entirely linked to each other. When a solid food is placed in the mouth, it is immediately subjected to several concomitant operations: mastication is central, helped by the action of saliva, tongue movements and inputs from other oral elements which ensure the sensorimotor control of these combined functions. During this set of combined and dynamic activities, many sensory attributes, pertaining to texture, aroma and taste, can be perceived and in turn sensory information is relayed to the central nervous system which can adjust the motor command. This chapter covers a description of the main oral elements and their activity during the food oral processing dealing with mastication and formation of a food bolus. Mastication is obviously the main oral activity in food oral processing but it is helped in this task by the action of the other oral elements, all working in coordination and not as unitary operations.

1 Physiology of Elements in the Oral Cavity

The human masticatory system consists of primarily of soft and hard tissues being the teeth, tongue, masticatory muscles and jaws. Other important organs or functions play prominent role in mastication, namely saliva, palate, cheeks, lips, for example in controlling food position inside the mouth and managing morsel positioning between teeth. Saliva, for its part, acts as a liquid glue, lubricating the mouth and reassembling all particles to form an aggregate that is safe for swallowing, as well as initiating chemical reactions associated with oral digestion.

1.1 Teeth

Teeth and their action during mastication are extensively documented as having adequate hardness and shape, being firmly rooted in the jaw bone to break, crunch and grind the food. Teeth are obviously essential elements for mastication and to a lesser extent, for swallowing. Teeth consist of crowns which protrude in the oral cavity and roots which are firmly inserted in the jaw bones. The crowns are coated with a layer of enamel which a high-mineralized tissue, able to concentrate stress and to resist to wear and fracture. A full dentition includes 32 permanent teeth evenly distributed on mandibular and maxillary arches. The tooth shape determines its function. There are three classes of teeth: incisors, canines and post-canines. Incisors are 8 front teeth and involved in biting act. Four canines have a cusp to tear up and pierce hard foods before crushing when food morsel is positioned in the region of the pre-molars and molars which are the sites of mastication of all solid foods. Among the 12 molar teeth, the 4 most posterior ones (wisdom teeth) are often absent or with delayed eruption and not involved in mastication. Premolar and molar crowns shaped with cusps act for crushing and mashing actions. Thus, the main mechanical actions applied on food by these post-canine teeth during mastication are compression and shear stresses. Achievement of correct mastication is dependent on the number of posterior teeth, active tools during comminution, and more precisely the number of pairs of antagonist teeth, namely functional posterior units (FPU). FPU appear to be a more pertinent indicator to evaluate oral health or masticatory potential in comminuting food than the total number of teeth (El Osta et al. 2014).

1.2 Jaws and Temporo-Mandibular Joints

The human masticatory system is constituted of two jaws supporting teeth. The upper jaw, the maxillae, is part of the skull. The inferior jaw namely the mandible is attached to the skull through 2 temporomandibular joints (TMJ) which serve as jaw displacement's guide. Each jaw supports the same distribution of teeth described above. The 2 TMJ are anatomically distinct yet functionally bound as they share the same jaw movements. The mandible can move as a result of forces from contraction of the masticatory muscles. Following alternance of muscle contraction and relaxation, the mandibular jaw is lowered then raised to open or close the mouth. Its movements are guided by the 2 TMJ. A large variety of translational and rotational movements is possible thanks to the characteristics of the attachment of the mandible to the TMJ, permitting extensive movements of the mandible in several trajectories (Koolstra 2002). These joints are characterized by a great complexity and importance in permitting rotatory movements (Ahamed and Dhanraj 2017). Mandibular movements can be recorded by various methods and are described according amplitude of displacement, angle, velocity, acceleration and duration of each position and phase, describing the jaw trajectory during each cycle constituting the masticatory sequence (Madhavan et al. 2018). Jaw movements are caused by forces generated by muscular contraction associated to reactive forces in joints, ligaments and teeth. Shape of posterior teeth and angle of cusp facets also plays a role in the direction of mandibular movements especially in guiding the jaw during the closing phase, the occlusion of each masticatory cycle (Wang and Mehta 2013).

1.3 Tongue

The tongue is a sensory and motor organ engaged in many oral functions (Doyle et al. 2022). It is a hardworking oral element continuously active during food oral processing, from food bolus formation to swallowing. It is a group of 17 skeletal muscles originating inside the tongue without a bone attachment (intrinsic) or originating outside the tongue (extrinsic). The contractile activity of these muscles during mastication participate in food management in the mouth providing an infinite variety of movements (Hiiemae and Palmer 2003). Tongue movements are complex and result from activities of some of these muscles which may act either jointly or in an antagonistic way. The tongue is positioned on the floor of the oral cavity and attached to the mandible, the process styloid and hyoid bones via its extrinsic muscles. The tongue occupies almost all the space inside dental arches. As the muscles of the tongue rapidly and precisely move in the mouth, they require a high level of control in response to stimulation or perception (Sawczuk and Mosier 2001). This high flexibility, as well as its size and shape adjustments, enables well-coordinated oral functions related to food, including mastication of solid foods, positioning the food between teeth and assembling the fragments, management and squeezing of semi-solid foods, and swallowing. Knowledge on the coordination of movements, oral activities and muscular contraction of the tongue is limited because of high complexity of measurements inside the mouth during functional activity (Sawczuk and Mosier 2001). Regarding the importance of the tongue coordination for smooth movements engaged in many functions among which the most important ones are mastication, swallowing, respiration and speaking, this organ is richly equipped in proprioceptors. Apart from this motor activity in conjunctions with food management, the tongue is also the organ involved in taste perception thanks to the numerous papillae recovering the tongue surface to fulfil the role of gustation (Doyle et al. 2022).

1.4 Salivary Glands and Saliva

Saliva is the whole buccal fluid lubricating the mouth and participating to bolus formation. It is predominantly produced by the three pairs major salivary glands, namely the parotid, submandibular and sublingual glands, and by the various minor salivary glands dispersed in the oral mucosae (labial, palatal, lingual and buccal mucosae). The saliva fluid is composed of at least 98% of water and also contains numerous electrolytes, glycoproteins, enzymes, immunoglobulins, plus many other products in very various quantities (Humphrey and Williamson 2001; Pedersen et al. 2002). Saliva is very critical for preserving the health of the oral tissues by continuously forming a lubricating coating layer aiding oral elements during mastication, speech and deglutition. Flow rate of saliva production varies in response to gustatory and mechanical stimulation. Saliva presents a normal range of pH between 6 and 7.5 and is characterized by buffer properties protecting the mouth against an aggressive environment. The normal daily production of saliva is about 0.5 to 1.5 L (Pedersen et al. 2002). The habitual flow is approximately of 0.3 mL/min in absence of or at low-level stimulation in most adults and can reach 7 mL/min under high-level stimulation, being highly dependent on the type of stimulation (Gavião et al. 2004). The large variations in flow and composition depend on oral activity and on the kind of stimulation. At rest, submandibular glands are the more active ones producing a viscous and mucin-rich unstimulated saliva. Sublingual glands contribute also producing a viscous saliva at rest. Salivary secretion, as well its composition, is entirely controlled by the autonomic nervous system, modulated by a reflex arc involving the salivation centre, and mostly stimulated by taste and mastication (Pedersen et al. 2002; Carpenter 2013; Proctor 2016). The salivary reflex is elicited by gustatory signals coming from chemoreceptors majorly located on the tongue. It is also triggered during mastication by activation of mechanoreceptors located in the periodontal ligament (Carpenter 2013), 5% of the normal masticatory forces being assumed to elicit mechanical saliva secretion (Gavião and Bilt 2004).

1.5 Masticatory Muscles

Mastication is operated by numerous skeletal muscles located around the skull whose contraction results in mandibular movements and the generation of forces needed to crush and manage the food in the mouth. Among them, the most powerful muscles are the masseter, the temporalis and the medial pterygoid, the first two being the most accessible covering their contraction, morphology, blood irrigation, for example (electromyography, tomography, echography, doppler, etc). In a simplified classification, they are referred as elevator muscles. In addition, the lateral pterygoid and the digastric muscles (anterior and posterior heads) are also important for jaw functioning and referred as depressor muscles. Opener muscles are described as depressor muscles while closers are identified as elevator muscles (Miller 2017).

The temporalis muscle is thin and fan-shaped attached to the skull (frontal, temporal and parietal bones) while the masseter presents a more complex organization in separate bodies which are attached between the zygomatic arch and the mandibular bone (Figure 1). The masseter and temporalis muscles are superficial while the medial pterygoid is located more deeply. Jaw closing muscles, such as the masseter, present a great complexity due to a multipennate and layered structure, segmented by aponeurosis. This structuration allows a greater number of fibres in a smaller cross-sectional area than other skeletal muscles in the body, thus providing a high potential for power and force in short displacements as well as many ways to contract differentially in response to the oral demand (Koolstra 2002; Miller 2017).

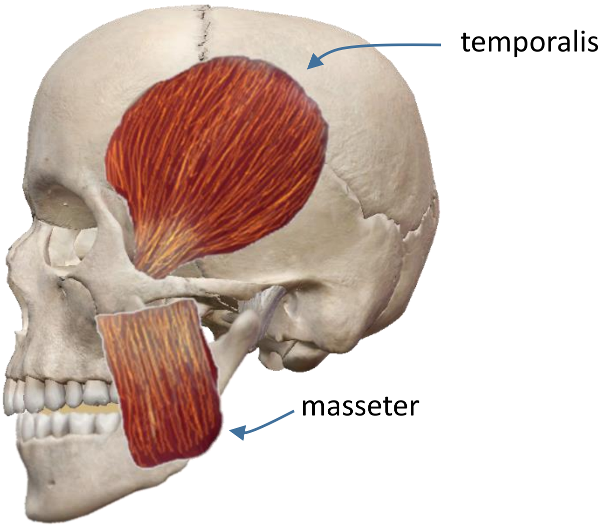


Figure 1: The main elevator muscles convenient for electromyographic recordings (EMG) during mastication. The masseter is inserted between the zygomatic arch and the body of the mandible. The temporal muscle is inserted between the parietal bone of the skull and the coronoid process of the mandible.

Regarding their structural organization, the masseter and the pterygoid muscles serve the primary role of producing force while the temporal muscles are be better suited to control jaw stability. A complex and harmonious alternation between contractions and relaxations of masticatory muscles generate mandibular movements that realize masticatory cycles. Contraction of muscles is finely controlled and highly coordinated to ensure the complex masticatory pattern displayed by mandible. A masticatory cycle is the result of successive recruitment of several groups of fibres inside a muscle or from different agonist muscles of which contractile activities are superimposed. The high level of complexity in coordination of masticatory muscles determine the direction of mandibular movement as well as a fine control of force applied, especially at the occlusal point.

Besides these active masticatory muscles, other head and neck muscles also participate to the masticatory activity, either actively or in postural and stability of jaw position (Giannakopoulos et al. 2018). Tongue, lip or cheek muscles also playing a determinant role during mastication because they participate in food fragments positioning, assembly of food fragments, mixing with saliva, and even bolus swallowing as described in other sections.

1.6 Other Oral Elements

The front and lateral walls of the mouth are controlled by the *orbicularis oris* (lips) and the buccinator (cheek) muscles. These muscles are active during mastication, helping in keeping food between teeth, they participate in gathering food particles and mixing with saliva during bolus formation. The buccinator muscle forms a part of the cheek and acts in coordination with tongue to force food morsels between teeth. Their contractile activity is synchronized with that of masseter muscle (Casas et al. 2003) and are active just at the beginning of the mouth closing (Dutra et al. 2010). Lip action prevents the food particles or the food bolus from slipping out of the mouth in case of mouth opening, and is also active during swallowing (Tamura et al. 2009). Pressure is the main characteristics of these muscles useful for comprehensive description of their role during mastication. Indeed, the strength of these muscles is important during mastication. A positive association between high perioral pressure and masticatory performance has been identified, as well as its role on bolus wetting and the time required for bolus formation (Mazari et al. 2007; Takahashi et al. 2013). Buccinator contraction has also been suggested to help saliva secretion (Kang et al. 2006). Central coordination is clearly required for the perfect monitoring of the complex activities of these oral elements during mastication without incidents such as biting tongue or cheeks (Takada et al. 1996). Moreover, the contractile activity of orbicularis and buccinator have been shown to change according to physical properties of food and thus confirmed the specific role of these muscles during mastication (Hanawa et al. 2008).

2 Control and Adaptation of Mastication

All oral motor activities (including muscle contraction along with functional jaw and tongue movements) require a fine control permitting biting, mastication, food oral management and swallowing. To accomplish this control and to adjust mastication parameters, the brain needs sensory information about what happens in the mouth. This information derives from various sensory organs distributed in oral structures. Sensory information is relayed to the Central Nervous System (CNS) which uses it in combination (superimposition, overlapping?) with the basic control of rhythm together with jaw reflexes.

2.1 Mechanoreceptors and Proprioceptors

The mouth is a very sensitive organ, densely innervated with nerve fibres and receptors involved in tactile perception and proprioception. During mastication, these receptors provide sensory feedback on events arising in the mouth during food transformation, feedback is also used for food texture perception (Lund 1991; Türker et al. 2007). A combination of inputs from all these receptors gives a complete image of what is perceived in the mouth in terms of food, food bolus properties and its position. Mechanoreceptors, as their name suggests, are sensitive to tactile and kinesthetic (*i.e.* during movement) stimulation such as constraints, stresses, strains, vibrations, pressures, slipping or flow. Many types of mechanoreceptors have been described in the oral regions, e.g. Meissner corpuscles, Ruffini and Krause endbulbs, Golgi organs, … etc (Avivi-Arber and Sessle 2018). Such receptors are arranged in the mouth to cover all types of stimulation and their regionalized location depends on the specific assignment or the oral element in perception. Mechanoreception is attributable to receptors located in the tooth supporting tissue, namely the periodontal ligament, in the hard palate, the cheeks and lips, the TMJ, and throughout the mucosae. Periodontal receptors are involved in the control of direction and intensity of forces (Trulsson 2006, 2007; Piancino et al. 2017). As a complementary sensitivity, proprioception encodes signals providing information on static position and movements. This sense is served by muscle spindles, arranged in the elevator and tongue muscles and signalling their stretching, Golgi tendon organs stimulated by muscle contraction, and also mechanoreceptors in the TMJ encoding for flexion and extension in the joint during movements. *De facto*, mechanoreception includes perception of food characteristics, while proprioception is more related to position, velocity and direction of movements, both types of perception playing an important role in the control of food oral processing since their combined inputs provide an overall and precise image of what is in the mouth, where it is positioned, in what state, together with a fine knowledge of level of contraction and position of oral structures (Foegeding et al. 2015). Proprioception has also been suggested to participate in swallowing initiation (Takeda and Saitoh 2016).

2.2 Neural Mechanisms

The fundamental pattern of mastication issues from a network of neurons, located in the brainstem, called the central pattern generator (CPG). The CPG is able to elicit the basic rhythmic activity of the jaw muscles independent of any descendant input (cortical) or sensory afferents coming from oral receptors (Lund 1991; Avivi-Arber and Sessle 2018). The CPG is composed of neurons mainly associated with the trigeminal system. Apart this autonomous rhythmic activity, it is controlled in a goal-oriented behaviour by inputs descending from higher centres in the brain (cortical areas), and the motor activity of mastication is also governed by mechanisms receiving peripheral feedback (Lund et al. 1998). Many orofacial muscles are represented in different cortical areas which can modulate the CPG activity. Additionally, the masticatory process displays large variation in the afferent inputs which provide feedback on the transformation of food in the mouth. This oral processing functionality relies heavily on peripheral feedback, which provides fine modulation to the basic pattern, generating an accurate physiological masticatory activity perfectly adjusted to oral events and the characteristics of the food/food bolus being processed (Lund and Kolta 2006). Thus, high variability in muscle contractions and the consequent jaw movements are the result of central commands by the CPG producing rhythmic activity modulated by inputs from the oral cavity. The range of muscle activation patterns and jaw movements offers many possibilities for optimization of masticatory strategies to food properties and individual characteristics (*e.g.* age or dental state) which are the main extrinsic sources of variability of masticatory pattern (Lund and Kolta 2006; Woda et al. 2006). During mastication, the CPG motor command is continuously and finely adapted to sensations arriving from the oral area and related to changes in food characteristics along bolus formation (Lund and Kolta 2006). Thus, among all these sensations, texture is the primary food property providing guidance to the motor commands defining the oral process thanks to the links between food structure and its perception.

2.3 Innervation of Muscles Involved in Mastication and Associated Oral Functions

The sensory information captured at the level of orofacial structures is transmitted to the CPG *via* the trigeminal nerve which is the fifth cranial nerve (CN V; Figure 2). This is a large and complex cranial nerve containing sensory and motor fibres. The CN V has ophthalmic, maxillary and mandibular branches, the former two containing sensory fibres only. The maxillary division of the CN V relays sensation from the face. The three branches converge on the trigeminal ganglion which contains the cell bodies of fibres. The maxillary branch carries sensory information from the upper region including the cheeks, the upper lip and the upper teeth, while the mandibular branch conveys sensory information from the lower area containing the lower lip, the lower teeth and the jaw (Figure 2). The motor part of the trigeminal nerve innervates the jaw opening and closing muscles, namely masseter, temporalis, pterygoid, mylohyoid and digastric muscles, and also conveying proprioceptive inputs from the TMJ (Yamada et al. 2005; Westberg and Kolta 2011).

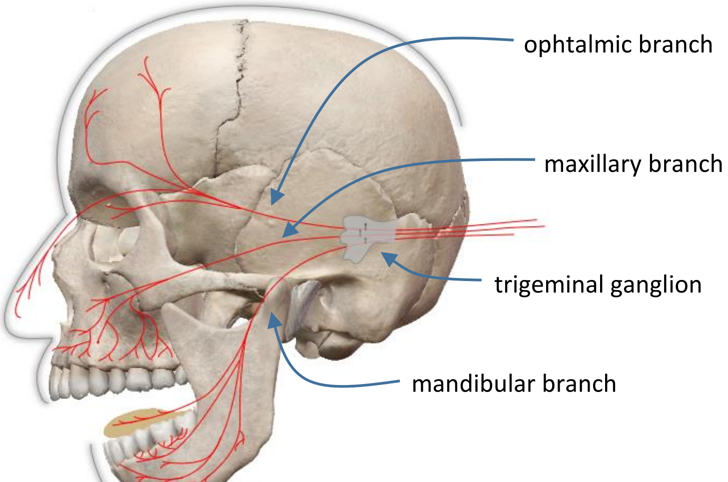


Figure 2: The trigeminal nerve is the fifth cranial nerve (NC V) containing sensory and motor fibres. It includes three divisions: ophtalmic, maxillary and mandibular branches converging on the trigeminal ganglion

Muscles responsible for tongue motility are innervated by motoneurons connected with the hypoglossal cranial nerve (CN XII) that only contains motor fibres and control all tongue movements. Activity of XII motoneurons is controlled by higher centres in the brain and also received, on the one hand, inputs from respiratory and swallowing centres, and on the other hand sensory information from the trigeminal (CN V), the glossopharyngeal (CN IX) cranial nerves. Considering that tongue is a major partner to the teeth during mastication, having even been identified as a masticator *per se*, other general sensations of the tongue, including taste perception, are transmitted through the facial, glossopharyngeal and vagus nerves which participate in sensory feedback and play an important role in coordination of tongue movements and other oral activities (Yamada et al. 2005; Hori et al. 2006). This coordination probably follows different ways depending on the role of the tongue either participating in particle gathering and bolus formation, to soft food squeezing against hard palate, or during swallowing (Lowe 1980; Taniguchi et al. 2013).

Facial muscles including those in cheeks and lips, are innervated by the CN VII for facial motor control. This nerve also presents a sensory function responsible in taste perception. There are many connections with other cranial nerves innervating the oral and facial area, and among them with all branches of the trigeminal one.

Activation of all these different groups of cranial motoneurons occurs during mastication and their precise coordination in performing this step is essential to ensure smooth operation of all the oral functions involved in food oral processing (Yamada et al. 2005).

2.4 Jaw Reflexes

Several reflexes can be described for the jaw motor activity and are responsible for the cyclic and stereotypical movement engaged in oral functions (Türker 2002). These jaw reflexes are generally considered as the base for governing the motor activity caused by muscle contraction and responsible for jaw movements. The main reflexes contributing to oral functioning are jaw-closing and jaw-opening reflexes (Lund and Olsson 1983). The jaw-closing, or jaw-jerk reflex, is a typical myotatic reflex beginning with the stretch of the muscles which activates the spindles located in the main elevator muscles (*e.g.* masseter or temporalis). The jaw-opening reflex is elicited in the jaw-opening muscles, such as the anterior digastric. It can be caused by a pressure applied on the teeth, a tap on the lips or pain in these tissues. Perception of a force applied to the periodontal mechanoreceptors signals a contact between antagonist teeth or contact with a food morsel. This elicits an increase in the jaw elevator muscle activity during biting or during the occlusion phase of the masticatory cycle.

The well-coordinated activation and inhibition of all jaw reflexes permits their efficient contribution to masticatory pattern which is required for smooth oral functioning (Yang and Türker 1999). Simple reflexes such as jaw-closing and -opening may be activated *per se* quite infrequently during normal oral functioning and only some of their components provide help to the oral complex functions (Dubner et al. 1978). Such reflexes contribute to oral motor activity in providing a stereotyped pattern which can be modulated and finely adjusted to oral perceptions. Sensory feedback from the oral receptors associated with inputs from the cortex level co-activate the CPG which can modulate the basic jaw motor pattern. Since masticatory muscles are able to generate very high levels of force, and teeth and tongue have to work together in a harmonized way, the jaw-reflexes contribute to a fine control of forces and movements, especially in protecting the oral structures from pain and damages during mastication.

2.5 Bite Forces and Masticatory Forces

In contrast to masticatory forces (exerted during mastication) bite forces relate to biting. In mastication the forces are exerted in a dynamic mode, alternating isometric (no change in muscle length) and isotonic (constant force with change in muscle length), while biting is generally applied as an isometric contraction during static exercises. In normal use, forces developed by the masticatory apparatus are caused by contraction of masticatory muscles and produce crushed food placed in the mouth. Variability of maximal bite force values depend on the recording device, the teeth considered and some other physiological factors, such as dental state, muscle strength, anatomy and neuromotor mechanisms; forces are generally higher in men than in women or with natural teeth compared to artificial ones (Koc et al. 2010). Nevertheless, independent to this variability, these measurements give an overall picture of what forces can be developed by the masticatory apparatus. The maximal force developed by the whole jaw possessing natural teeth is about 60 to 75 kg, (*i.e.* 590 to 740 N) (Gibbs et al. 1981). When measured for a pair of antagonist teeth, values relate to the location on the arch and also probably to the teeth shape (Carlsson 1974). The greater values ranging from 300 to 600-700 N have been measured in the first molar section which corresponds to the region of masseter attachment (Fløystrand et al. 1982; Hagberg 1987; Bakke et al. 1990). Lower values of maximal bite force have been recorded in the more anterior teeth, around 300-400 N for the premolars and canines, and about 100 to 200 N for the incisors (Ingervall and Helkimo 1978; Haraldson et al. 1979; Hagberg 1987). Masticating with the posterior teeth requires less energy when compared to the anterior teeth. Indeed, to reach a given functional force with anterior teeth, a greater muscular activity would be required due to the mechanics of the TMJ working like a lever (Devlin and Wastell 1986).
Bite forces are estimated to represent only a small percentage of the maximal forces that can produce the masticatory apparatus (Gibbs et al. 1981) but these later are not easy to record during movement and dynamic events elicited during mastication and only approximation can be extrapolated from muscle contraction recordings during functional mastication (Ferrario et al. 2004).

3 Oral Processing of Food

Food oral processing encompasses many various oral elements and functions including breaking and masticating the solid food thanks to jaw movements activated by contraction of masticatory muscles, mixing of food fragments with saliva, tongue movements placing the food between the active teeth, or to compress soft food against the hard palate, etc. All these activities share the common objective of preparing a food bolus with characteristics favourable to a safe and secure swallow without pain or increased risk of dysphagia. Since food oral processing is a recent and fast-emerging research area, some famous reviews have organized an abundant literature in this area combining physiological and food perspectives (Wang and Chen 2017; van Eck et al. 2019; Guo 2021; He et al. 2022). Taste, tactile and kinaesthetic perception, as well as oral digestion, are also important functions associated with food oral processing. All these activities can be considered as part of the food oral processing and can be evaluated through various methods which are implemented either to study physiology or health of oral function or to study adaptations to food changes.

3.1 Principal Methods for Studying Food Oral Processing

Different methods used to study the oral functions and food oral processing mostly relate to movements and forces/pressures generated by or on oral elements during mastication, tongue movements or swallowing, which can be combined with the study of the characteristics of the resulting food bolus and to characteristics of saliva production (Liu et al. 2022).

3.1.1 Forces and Muscular Contraction Recordings

Bite Force

The recording of bite and masticatory forces have received considerable attention for a long time and many reports can be found in literature. Generally, measurements can be made with electrical devices (of varying complexity) placed between a pair of antagonist teeth or section of teeth. Today, electronic devices provide accuracy and precision (Fernandes et al. 2003; Koc et al. 2010; Liu et al. 2022). Masticatory forces are more difficult to measure accurately since they are developed during dynamic conditions, and inserting atransducer inside the working mouth can disrupt mastication. Despite these technical difficulties, masticatory forces have been shown to depend on food hardness. Values around 19 N have been reported for mastication of cheese between 20 N and 50 N for bread, and approximately 50 N for carrots or peanuts (Michael et al. 1990). When measured on the whole dental arches, values were greater than measured on a dental section, around 220 N for cheese and 350 N for peanuts (Gibbs et al. 1981). Significant correlations have been obtained between the bite force and the masticatory performance (Okiyama et al. 2003). This difficulty in force measurement has favoured the emergence of electromyography as a method to address masticatory force through recording muscular contraction under the dynamic conditions of mastication. Muscular contractions are the result of electrical activity in the muscle fibres and on the oral level, responsible for multiple masticatory movements of the jaw and tongue.

Electromyography

Difficulties in force measurement has favoured the emergence of surface electromyography (EMG) which address masticatory force through muscular contraction recorded under dynamic conditions. Surface EMG is a non-invasive technique and has been largely applied in food oral processing studies thanks to its ease of use (González et al. 2001; Gonzalez Espinosa and Chen 2012). During muscle contraction, EMG electrodes record global electrical activity, namely the motor unit action potentials generated in muscle fibres which have been filtered by tissue (Gonzalez Espinosa and Chen 2012). The relationship between EMG and forces is linear in isometric muscular contraction, thus relationship between EMG signal and force generated is neither direct nor simple. The relationship between EMG and bite forces can be linear in isometric contraction under well-controlled recording conditions, but neither direct nor simple during mastication mixing different muscular contraction modalities (isometric and isotonic) and jaw displacements. Nevertheless, it provides access to physiological mechanisms causing muscle contraction and movement, along with the resulting force generated during physiological function (Lindauer et al. 1991). EMG signals can be impacted by physiological parameters (motor unit recruitment, temperature, skin surface properties…) and by technical parameters such as electrodes type or placement, filters, signal amplification (Gonzalez Espinosa and Chen 2012).

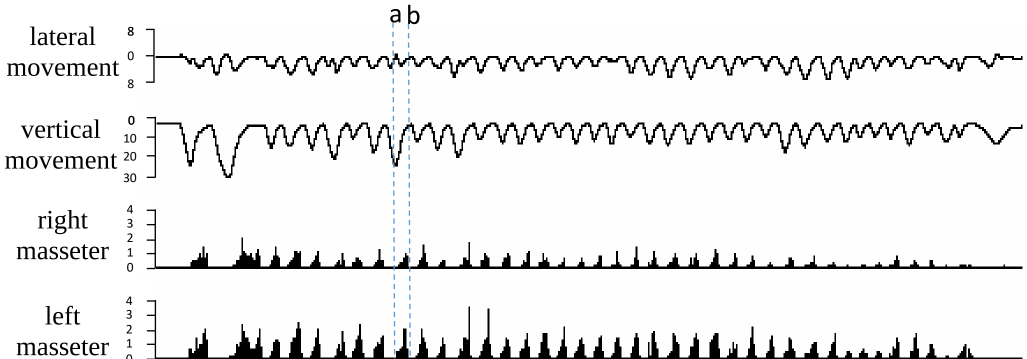


Figure 3: Example of electromyographic recordings (EMG) from right and left masseter and temporalis muscles, and vertical and lateral mandibular movements during a complete masticatory sequence. Dotted lines, noted a and b, delineate a single masticatory cycle, with the beginning (a) and the end (b) of jaw closing, corresponding to a burst of action potentials in each elevator muscles being contracting to face the food. Jaw movement is expressed in mm and muscle contraction in mV.

As force is generated to break the food morsel, the masticatory muscle contraction reflects several useful indications on how the food is perceived in mouth and how the masticatory system is programmed to breakdown and form the bolus. The main masticatory muscles accessible for EMG recordings during mastication are the masseter, temporalis and digastric muscles (Figure 3). Some publications also report EMG measurements of buccal and lingual contractile activities (Casas et al. 2003; Hanawa et al. 2008). Thus, despite some limitations in the technique and a real risk of mistakes or misinterpretations, EMG presents great interest in the assessment of oral function for integrative access providing rich-information on how the food is managed during mastication, and how the masticatory apparatus adapts to oral processing of specific foods (Lassauzay et al. 2000; González et al. 2001). After several steps in the raw data processing, some useful variables may be extracted from the recordings, namely the total duration of the masticatory sequence, the number of masticatory cycles, the total muscle activity for the whole masticatory sequence (sum of area of rectified EMG signal of each masticatory cycle), the average of the activity of contraction per cycle, amplitude of the contraction, etc which can be analysed in link with food characteristics and their perception (Lassauzay et al. 2000; Peyron et al. 2002; Woda et al. 2006; Gonzalez Espinosa and Chen 2012; Kazemeini et al. 2021).

3.1.2 Methods for Mandibular Movement Recordings

Any movement of the mandible is a consequence of contraction of masticatory muscles within the constraints of the temporomandibular joints (TMJ) which facilitate a large variety of movements. During the masticatory sequence, contraction of elevator muscles (*e.g.* masseter muscles) occurs during mouth closing to crush the food. Thus, for a more complete and dynamic analysis of food oral processing, EMG and mandibular movements are often recorded simultaneously. Several methods, from simple to advanced ones, can be employed to record these jaw movements. Most such recordings operate with a sensor attached to the mandible. Such sensors work on a physical principle for example accelerometers, electromagnetic inductance, optoelectronic elements related to a mechanical, graphical, telemetric, magnetic, opto-electronic, videography, ultrasonography (Lepley et al. 2011; Madhavan et al. 2018). Numerous parameters can be extracted to characterize the jaw movements in terms of amplitudes, velocities, duration of each period of the masticatory cycles, or of the complete masticatory sequence, and provide a wide range of information on the dynamic of what happens in the mouth while forming the food bolus (Chew et al. 1988; Horio and Kawamura 1989; Peyron et al. 1997). In some clinical conditions, these advanced techniques cannot be used directing researchers to less invasive method such as videography whose use has been validated against EMG (Hennequin et al. 2005). The major limitations in recording human jaw displacements is embodied when physical elements are placed inside the mouth and interfere with normal movements, perception and mastication control. EMG and movements recording combination provide data on the muscular activity in each mandibular position and for each phase of the masticatory cycle.

3.1.3 Tongue Movements and Tongue - Palate Pressure Recordings

Tongue movements can be followed, through videofluorography (an X-ray technique requiring mixing food with a radio opaque contrast medium), ultrasounds or functional magnetic resonance imaging (fMRI) (de Wijk et al. 2006; Okada et al. 2007; Taniguchi et al. 2013; Genna et al. 2021). These recordings provide data on the functional contribution of the tongue, and other oral structures, to the different events occurring during food management, food bolus formation and the early phase of swallowing initiation, as well as location of the food at any time during the masticatory sequence (Mioche et al. 2002). Horizontal and vertical dimensions of the tongue present different amplitudes during the different phase of mastication and are also dependent on food consistency (Taniguchi et al. 2013). Functional magnetic resonance imaging has been useful to provide a visual description of specific tongue muscle contribution during swallowing (Gassert and Pearson 2016). Oral movements of the tongue have been explored via an ultrasound method that linked perceived sensory attributes (de Wijk et al. 2006).

In addition, many methods have been developed to assess intraoral tongue pressure, such as small pressure sensors embedded in a palatal appliance or in a denture, or air pressure measured in a balloon compressed by tongue, the Iowa Oral Performance Instrument (IOPI, Oakdale, Breakthrough) or other hand-held pressure sensors (Youmans and Stierwalt 2006; Engelke et al. 2011). All these methods have been used with the same general objective which is the analyze of the tongue behavioral contact with palate, including analysis of its position, what areas are in contact and what is the pressure exerted by tongue against the palate, during food oral processing as well as with a focus of its role in swallowing (Ono et al. 2004; Hori et al. 2006; Kieser et al. 2011; Funami 2016). Another item of information often recorded is the maximum isometric tongue pressure (MITP), which is generally reported with values between 10 kPa and 70 kPa (Youmans and Stierwalt 2006; Utanohara et al. 2008; Alsanei and Chen 2014). As observed for masticatory muscles, the MITP values are higher for men than for women, and decrease with advance in age (Youmans and Stierwalt 2006; Utanohara et al. 2008). The biomechanical coordination of tongue and jaw movements is described according the phase of the masticatory cycle with tongue pressure occurring during the occlusal phase (opposite teeth in contact) with a quick peak just before jaw opening (Hori et al. 2006). It has also been used to describe food oral processing and its specificities according to the food characteristics or when tongue is involved in food oral processing of soft foods which are squeezed against the palate (Nakazawa and Togashi 2000; Koç et al. 2013; Yokoyama et al. 2014; Funami 2016; Nishinari et al. 2020).

3.1.4 Saliva Sampling

Given the importance of saliva in the many aspects of oral function, besides maintaining oral health, its characteristics are interesting across several dimensions. Measuring saliva flow or composition or viscoelastic behavior, for example, are needed to obtain normal reference values. Assessment of variations in saliva properties depending on individual characteristics or environmental conditions such as food features or type and moment of collection, for example, are important in food oral processing studies. Whatever the context or the objective of the sampling, saliva collection is a non-invasive technique. Several methods for saliva collection are described in literature (Navazesh and Kumar 2008). Resting saliva flow, which is saliva produced in absence of any source of stimulation, is allowed to drain in a receptacle and the flow estimated by volume or weight and reported over a sampling period. This unstimulated saliva can also be recovered by spitting by the participant. Suction tubes, cotton rolls, strips or technical papers can also be placed on the floor of the mouth to absorb saliva.

This later method can also be used to estimate saliva coming from minor salivary glands (Shern et al. 1990). Saliva collection during gum chewing or citric stimulation produces a larger quantity of saliva and is referred to as stimulated flow. In order to collect saliva from individual major glands, a cotton roll can be placed at the orifice of a selected gland but, in addition, specific devices with an instrument directly connected to that gland duct are useful (Navazesh and Kumar 2008). Several studies have reported results on the reliability and reproducibility of these methods, irrespective of the high degree of variability due to individuals, time of the day at which it is collected, stimulation mode or the circadian rhythm (Navazesh and Christensen 1982; Fontana et al. 2005). Nevertheless, maintaining or verifying the stability of saliva during its collection and its use is a crucial challenge to face in food oral processing studies. Indeed great vigilance is required to ensure reliable results regarding salivary amylase activity, viscosity, biochemical composition, pH, etc, that is either for biochemical assessment of saliva but also to study its role in food bolus formation or perception (Ngamchuea et al. 2018).

3.1.5 Food Bolus Characterization

Apart the fact that the food bolus produced by mastication is a heterogeneous material, the choice of method used for its characterization is driven both by the objective of the study and specificity of the characteristics being measured. This choice is pertinent since outputs can be used to assess both texture perception and mastication adjustment along the physiological process.

Food bolus characteristics depend on the initial nature of the food matrix and, whereas it undergoes continuous deformation during mastication, it also depends on the masticatory stage for which the bolus is considered (between first bite and swallowing). A plethora of methods have been developed to cover the different physical and biochemical dimensions of food bolus features (Panouillé et al. 2014). The main ones concern the physical aspects of the bolus playing a key role in swallowing, namely particle size, rheological behavior and level of saliva incorporation.

Bolus particle size is the most frequent measurement reported in the literature. Sieving or image analysis, bolus has been described with the number of particles, their size distribution and the median, or particle shape (Jalabert-Malbos et al. 2007; Rodrigues et al. 2014). As bolus formation involves simultaneous fragmentation and lubrication of fragments, methods giving access to rheological description and level of hydration are undoubtedly useful. When these measures are performed on the food bolus collected just before swallowing, they provide knowledge of the quality that the bolus must meet for a safe-swallowing (Peyron et al. 2011). Many varied methods such as the texture profile analysis (TPA test), compression test or oscillatory rheometry, to name a few, have been chosen for food bolus characterization depending on the nature of the food matrix and on the objective of the measure (Panouillé et al. 2016). Tribology is another phenomenon considered for food bolus characterization giving access to the degree of friction in the mouth in relation to oral lubrication (Shewan et al. 2020; Sethupathy et al. 2021). Bolus hydration is an interesting variable, linking food structure and mechanisms of bolus formation, which impact on rheological behavior and swallowing. With a purpose of studying the role of the oral phase in digestion and nutrition, several biochemical analyses can be conducted on the bolus, such as alpha-amylase activity, presence of nutrients or of molecules signing the initiation of oral digestion (Freitas et al. 2018; Blanquet-Diot et al. 2021).

Obviously, a combination of different methods characterizing several dimensions of the food bolus could be interesting to gain complementary information about this complex material. Whatever the method used, it should be used and interpreted with caution due to the complex nature of the food bolus and the dynamic mode of its formation.

3.1.6 In Vitro Simulation of Mastication

Several devices have been developed for in vitro food oral processing studies. Most of these have been conceived on the basis of the food breakdown into similar sizes to what is observed in natural mastication (Salles et al. 2007; Woda et al. 2010). These devices make it possible to control of some masticatory variables such as the number of masticatory cycles, the force applied, a dynamic saliva addition and some movements simulating particles gathered by the tongue. They are mainly operated with the final objective of providing bolus with particle size characteristics comparable to the *in vivo* bolus. These devices also provide access to oral mechanisms, sometimes complex, which address in vivo studies such as the effect of oral processing on flavor release (Salles et al. 2007) or the role in nutrition (Peyron et al. 2019). Furthermore, simulation models provide interesting access to analyse specific oral deficiencies on food structure disruption, bolus formation, and as bolus at swallowing, avoiding in vivo clinical trials potentially dangerous for frail individuals. Other interesting systems have been proposed to analyze oral behavior of soft or semi-solid foods (Prinz et al. 2007; Raja et al. 2022).

3.2 Influence of Oral Physiology on Food Oral Processing and Food Bolus Formation

3.2.1 Food Oral Processing

Food oral processing is a dynamic process covering management and process of a food placed in the mouth and requiring several physical transformations to be suitable for swallowing; the resulting material being called the food bolus (Figure 4; Chen 2009). The physical transformation operated during food oral processing refer to a combination of physical fragmentation, lubrication with saliva and management of oral transport of food material at all times of the oral stage from biting to swallowing (Mosca and Chen 2016; Wang and Chen 2017; Guo 2021). The major oral functions accountable for these operations are mastication, salivation and tongue activity, the degree of involvement of each factor varies according to the nature of the food, for example the degree of solid or semi-solid consistency (de Wijk et al. 2011; Nishinari and Fang 2018). The initiation of digestion for some foods also occurs during food oral processing (Bornhorst and Singh 2012; Blanquet-Diot et al. 2021). Food oral processing involves the activity of all oral muscles, including the tongue, jaw movements and saliva provision, all contributing to the preparation of a food bolus for safe swallowing. This process reflects interactions between oral structures and food characteristics, their dynamic interdependence being the main factor governing the food oral processing. When a food is placed in the mouth, every component constitutes a set of stimuli which are perceived by all receptors dispersed in the oral tissues. Sensory information is conveyed toward the central nervous system which respond by a motor command to the masticatory muscles strictly adjusted to the initial set of stimuli (Lund and Kolta 2006). The global motor response is expressed through the masticatory act which relates to the food perceived and analyzed in the mouth. Characteristics of the oral structures such as dental state, saliva flow, tongue motility, muscular potential, are factors influencing the food oral processing in terms of particle fragmentation, saliva provision and gathering food fragments in a food bolus safe for swallowing (Chen 2009). Plenty of physiological inputs occurring during food oral processing are converted into sensory signals at any moment of food transformation and serve both as indicators to continue adjustment of motor activity but also to offer sensory perception of food characteristics (Wilkinson et al. 2000; Salles et al. 2010; Koç et al. 2013; Pascua et al. 2013; Foegeding et al. 2015; Nishinari and Fang 2018).

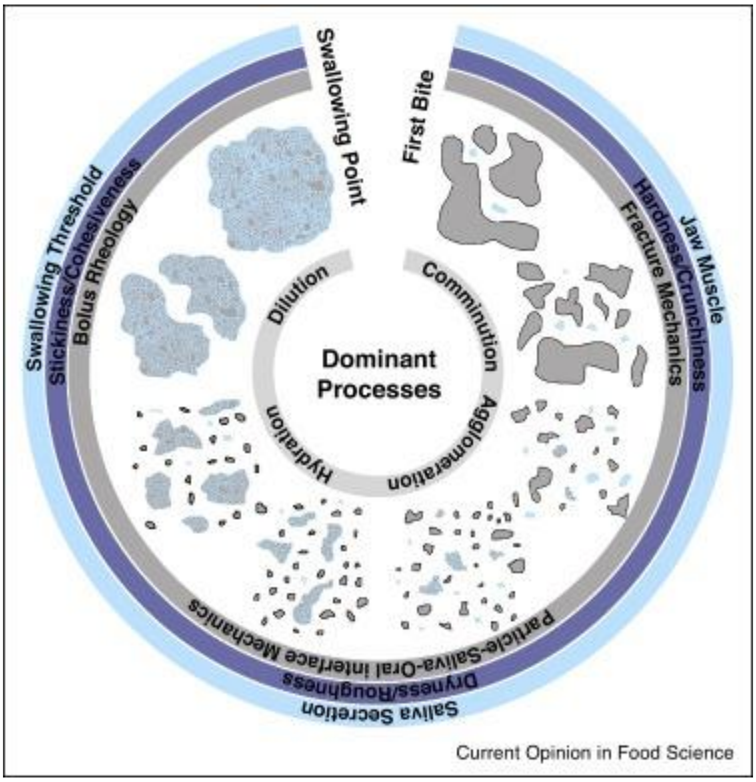


Figure 4: Schematic illustration of mechanisms involved in food oral processing from first bite to bolus swallowing. Rings represent major processes regarding particle size reduction and food-saliva interaction, together with physiological elements involved and main physical dimensions which can describe the food bolus along the process. A full description can be read in the related publication (Witt & Stokes, 2015, with permission).

3.2.2 Food bolus characteristics

Apart from an influence of oral physiology, the food bolus characteristics relate to mechanisms of solid food fragmentation under the action of the teeth, namely breakage function and food-saliva interactions (Figure 4). The food bolus is unsurprisingly a heterogenous and complex material with various physical properties continuously varying during the entire oral transformation whether the food is solid or semi-solid. Fracturing which is a major mechanism during mastication is dependent on initial physical properties of food as well as its geometry, fracture propagation, composition, interactions with saliva (Lucas et al. 2002; Swackhamer and Bornhorst 2019). Thus, many different physico-chemical dimensions can be described for a food bolus, the most important ones relating to rheological behavior, saliva impregnation and fragmentation level (Panouillé et al. 2016). Softening, reduction in size, hydration and cohesion or plasticity are common physical characteristics for bolus of most swallowable boluses, even if different kinetics or patterns are described depending on food structure (Jalabert-Malbos et al. 2007; Peyron et al. 2011; Loret et al. 2011; Stokes et al. 2013; Larsen et al. 2016; Gao et al. 2018). The particle size generally decreases as the number and area of particles increases along the progress of the masticatory sequence (Le Bleis et al. 2013a). As particle size is one of the main requirement that the bolus must meet to be safely swallowed, it is not surprising to observe similar size distribution in boluses of a given food (Peyron et al. 2004b; Jalabert-Malbos et al. 2007). Bolus lubrication generally increases with addition of saliva which is mixed with fluids coming from food matrix such as juice or oil, oily or moisture foods needing less saliva incorporation than dry foods for example (Drago et al. 2011). In addition, bolus can be characterized in many other dimensions covering lubrication relating to the rheology and surface properties, as well as recoverability or plasticity to facilitate slipping during swallowing (Stokes et al. 2013). Indeed, saliva is a complex biological fluid presenting unique rheological characteristics. Its incorporation in the food bolus changes rheological and tribological properties of food through hydration and also hydrolysis of some food components. For example, this decreases viscosity of food bolus, increases bolus consistency, leading to a stretchable and deformable material as required for safe swallowing. At the same time, and since food particles interact with surfaces of all oral elements, saliva is clearly useful in reducing the frictional forces resisting to movements during mastication and swallowing, avoiding particles to escape from the bolus (Le Bleis et al. 2013b; Mosca and Chen 2017; Khramova and Popov 2022)

3.2.3 Role of Saliva

In addition to the diverse aspects of its function in preservation of oral health, saliva strongly participates in food oral processing, food bolus formation and digestion. Despite great variations between individuals' flow rate or composition (Heintze et al. 1983; Humphrey and Williamson 2001; Dodds et al. 2005; Zussman et al. 2007; de Almeida et al. 2008), the rheological properties of saliva are key during food management and bolus formation (Pedersen et al. 2002; Bongaerts et al. 2007; Mosca and Chen 2017; Boehm et al. 2020). The specific rheological properties, especially viscosity, allow a rapid spreading of saliva both on the oral surfaces and on the food fragments (Schwarz 1987; Drago et al. 2011; Carpenter 2013; Boehm et al. 2020). In this way and in association with its composition, saliva also contributes to food breakdown through mechanical and biochemical actions. During mastication, a film of saliva protects oral tissues and helps in reducing friction. Food fragments produced by action of teeth are mixed with saliva as soon as they are formed. Addition of saliva serves in coating food fragments, moistening them and aiding their agglomeration. Additionally, and in combination with dissolution of some constituents as well as mixing with food liquids, these actions provide a specific rheological environment to the bolus. Lubrication favors food softening and acts in particle gathering, it also exposes food constituents to salivary components such as alpha-amylase which acts in degrading food and modifying rheological properties (Mosca and Chen 2016; Boehm et al. 2020; Pu et al. 2021). Participating to bolus formation, saliva also importantly contributes to food textural perception through mechanical disruption and enzymatic reactions causing food breakdown (Janssen et al. 2007; Mosca and Chen 2017; Laguna et al. 2021) besides taste perception for which the liquid phase is essential. Apart from the level of food breakdown, initiation of swallowing is also strongly linked to the degree of lubrication of the food bolus (Coster and Schwarz 1987; Pedersen et al. 2002; Chen and Lolivret 2011; Tobin et al. 2020). At the end of mastication, the level of lubrication ensured by saliva addition initiates swallowing of a food bolus characterized by strong cohesive forces between the food particles (Figure 4; Prinz and Lucas 1995; Chen and Lolivret 2011; Mosca and Chen 2016; Boehm et al. 2020; Liu et al. 2020).

Saliva deficiency has been shown to increase the duration of mastication, insufficiently soften food bolus, disturb swallowing or reduce perception of taste (Hamlet et al. 1997; Peyron et al. 2018).

3.2.4 Role of the Tongue

Besides a role of the tongue in taste perception, food oral processing depends on actions of the tongue first in moving the pieces of food toward the posterior teeth with a pullback movement. During mastication the tongue remains very active to place food between the teeth, to sort out the food fragments before each occlusion for further crushing, to gather particles into a rounded mass called the bolus, to favor mixing with saliva, and to prevent food parts from escaping.

All these tongue movements are coordinated with jaw displacements. Mastication comes to an end when the food bolus structure has been sufficiently disrupted, and the tongue serves as an actor for transition towards swallowing by playing a major contribution in oral and pharyngeal phases of swallowing. The tongue acts to position the food in posterior area of the mouth so it can be safely swallowed and progressively squeezes against the hard palate. It imparts peristaltic movements and pressure to place the bolus in the direction of the pharynx and then retracts to move the bolus down in the pharynx and esophagus (Hiiemae and Palmer 2003; Youmans and Stierwalt 2006; Kieser et al. 2011; Nishinari et al. 2020). During swallowing, the tongue is in contact with both the hard and soft palate and its shape, area and contour are adjusted to bolus volume (Kahrilas et al. 1993).

The role of the tongue in mastication and swallowing is well-documented with substantial amount of literature on tongue strength and consequences of deficiencies on its performance (Ono et al. 2004; Clark and Solomon 2012). Apart its role on bolus formation, mastication has significant influence on taste perception since responsible in release of taste compounds by breaking the food matrix and increasing access to taste receptors (Salles et al. 2010; Liu et al. 2017).

3.2.5 Interindividual Variability in Food Oral Processing and Food Bolus Characteristics

Individuals develop different strategies for oral processing, according to their oral physiology and specifically the main features of the physiology of mastication (Gibbs et al. 1982; Brown et al. 1994). This large variability between and among individuals are observed independently the food characteristics and expressed for example in the number of masticatory cycles, the duration of the masticatory sequence, the masticatory frequency, the amplitude of muscular contraction and force generated for a given food (Brown et al. 1994; Lassauzay et al. 2000; Peyron et al. 2004a; Woda et al. 2006). Important differences have been observed in several masticatory parameters between males and females masticating the same food, males developing for example greater muscular contraction, with larger vertical amplitude and velocities during mandibular movements related to a larger oral cavity, finally using different food oral processing strategies (Ketel et al. 2020; Rosenthal and Philippe 2020). Maximal tongue pressure has also been reported to greatly vary between individuals (Loret et al. 2011; Alsanei et al. 2015; Pematilleke et al. 2021). In contrast, individuals clearly display reproducible patterns of masticatory process for a given food chewed on different repetitions or occasions (Lassauzay et al. 2000). Wide variations in masticatory strategies between normo-dentate individuals for a given food have their rationale in the common need of producing a safe swallowable food bolus, in terms of granulometry as well as rheological behavior, which has been verified for several foods (Woda et al. 2006; Loret et al. 2011; Pematilleke et al. 2021).

3.2.6 Impact of Ageing on Food Oral Processing

The consequences of ageing on food oral processing has been largely investigated and despite the heterogenicity of elderly population, some common characteristics have been highlighted. In brief, ageing alone has little impact on masticatory performance or on the ability of old people to fragment food in smaller particles and to make a smooth and cohesive bolus (Feldman et al. 1980; Ikebe et al. 2011, 2012). Several physiological changes progressively adapt the oral sensorimotor functions to ageing so that the purpose of mastication in providing a safe bolus for swallowing is achieved. For example, without any gender difference but great interindividual variability, tongue strength appears to be lowered in elderly even if no clear decrease has been observed for swallowing pressure (Taniguchi et al. 2008; Fei et al. 2013; Alsanei and Chen 2014; Kim et al. 2021). Maximal bite force and masticatory muscle mass have been found to decrease with age (Bakke et al. 1990; Newton et al. 1993; Hatch et al. 2001; Yoshida and Tsuga 2020). The total number of masticatory cycles performed for a given food increases with age probably to reach the same amount of saliva impregnation in the bolus, but masticatory frequency is preserved (Figure 5; Peyron et al. 2017; Aguayo-Mendoza et al. 2020). This has an impact on the total EMG activity which increases *de facto* (Peyron et al. 2004a; Park et al. 2017). In contrast, the same level in masticatory muscle contraction (EMG activity) is produced during individual masticatory cycles when correct oral conditions are maintained, and this despite an association between sarcopenia and masticatory function (Figure 5; Kohyama et al. 2002; Peyron et al. 2004a; Yoshida and Tsuga 2020). Amplitude and velocities in mandibular displacements significantly decrease with age even with good oral state (Karlsson and Carlsson 1990). In contrast, the masticatory frequency does not undergo significant changes during ageing but neither particle size distribution at least for some foods (Peyron et al. 2004a; Mishellany-Dutour et al. 2008).

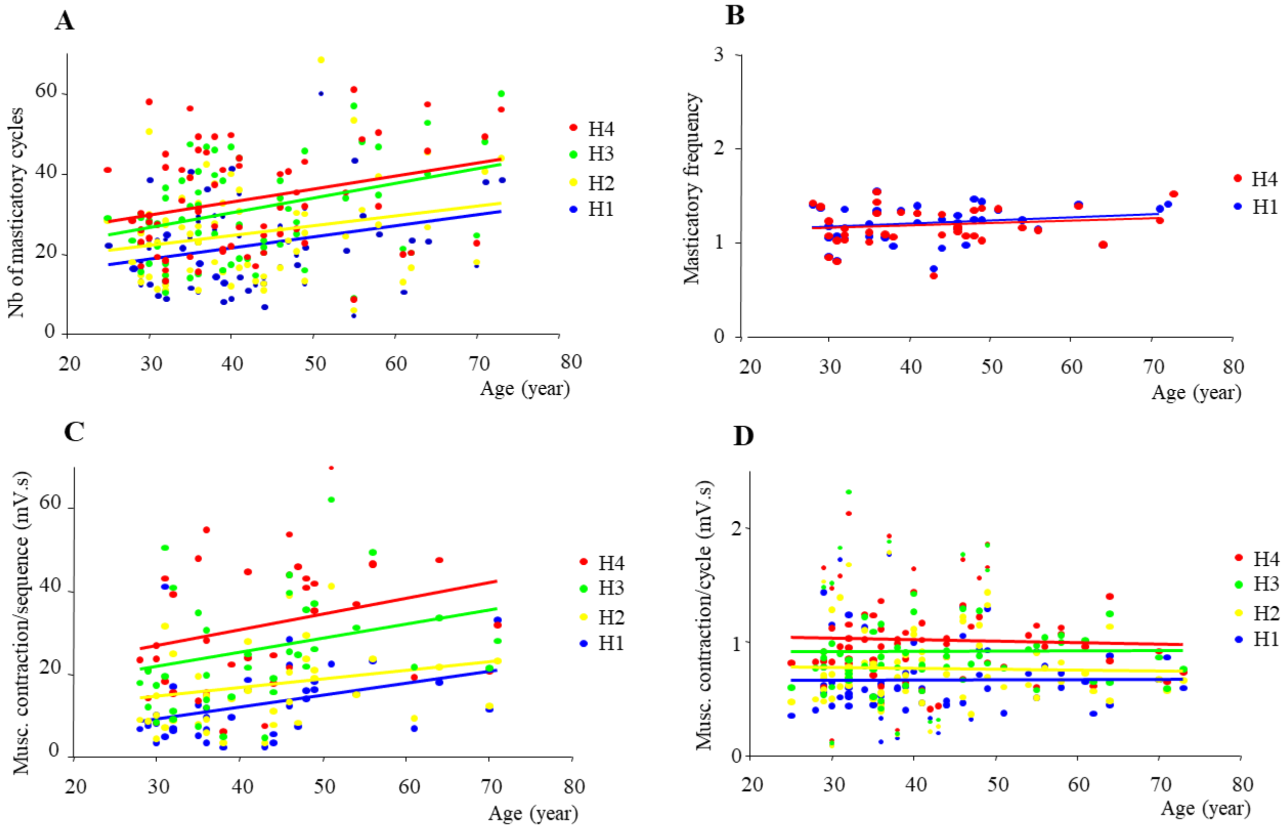


Figure 5 : Effects of healthy ageing (25-72 years) and hardness of an elastic food model (softest H1 to hardest H4) on number of masticatory cycles (A), masticatory frequency (B) and muscular contraction recorded by electromyography (EMG) for the complete masticatory sequence (C) and for a single masticatory cycle (D). Data for all individuals and 4 hardness are presented except for masticatory frequency (B) where only data for H1 and H4 are presented for better readability. (modified from Peyron et al 2004, with permission)

3.2.7 Impact of Tooth Loss and Oral Deficiencies on Food Oral Processing and Food Bolus Characteristics

Ageing is frequently associated with dental loss, and masticatory function is largely impeded when teeth are missing (Ikebe et al. 2012; Fan et al. 2022). The number of teeth, the number of posterior antagonist teeth (or posterior functional units) and the quality of opposite teeth contacts during mastication are determinant factors for mastication functioning as well for food comminution (Kohyama et al. 2003; Hennequin et al. 2015; Huang et al. 2021). When teeth are missing, most of the sensory feedback normally coming from dental mechanoreceptors is reduced and the necessary modulation of oral motor activity is partial and improper (Veyrune and Mioche 2000). In denture wearers, masticatory strategies associated with lower and imprecise masticatory forces are generally characterized by a decrease in masticatory frequency, a lack in the adjustment of muscular activity to food hardness. Facing their bad oral conditions, they try to compensate missing teeth or inaccurate occlusion by increasing the number of masticatory cycles often without success in reaching the optimal particle size level for a safe swallowing (Figure 6; Woda et al. 2006, 2011; Veyrune et al. 2007;

Mishellany-Dutour et al. 2008). Oral deficiencies such as tooth loss constitute a steady impairment at various levels of food oral processing, resulting in an incomplete fragmentation and disorganized food bolus (Figure 6), or inadequate softening, before swallowing, and this is particularly important in case of cumulated oral deficiencies (Yven et al. 2006; Mishellany-Dutour et al. 2008; Peyron et al. 2018).

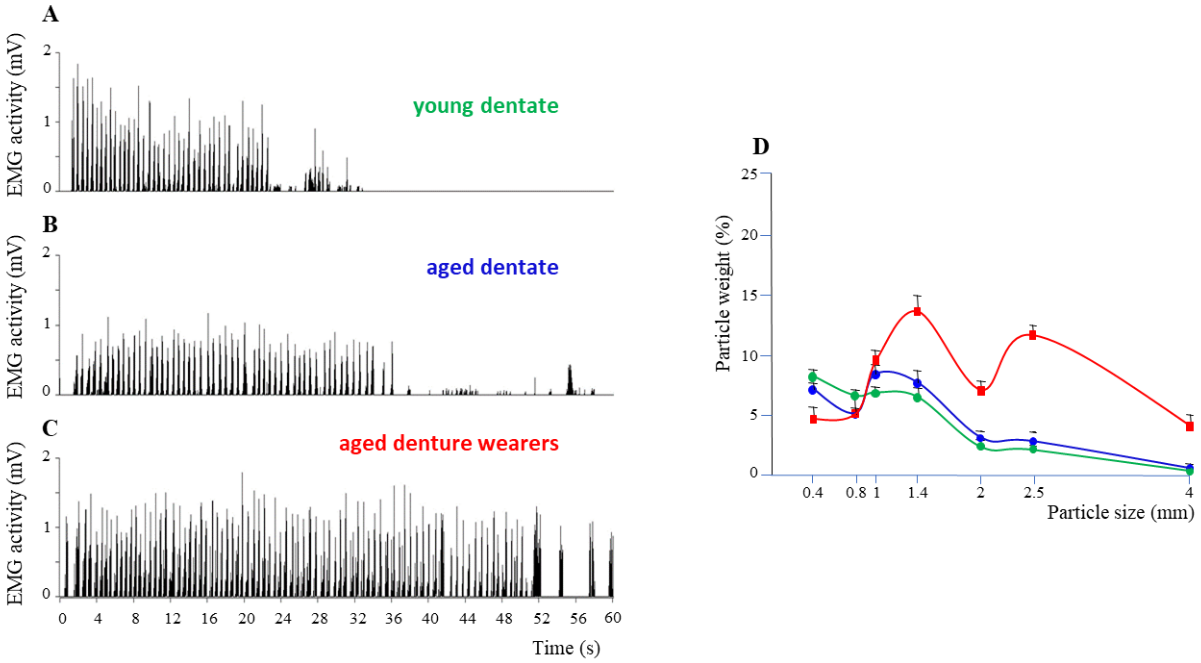


Figure 6: Examples of electromyographic (EMG) activity recorded for the right masseter muscle during mastication of peanuts in a young dentate (A), an aged dentate (B) and an aged denture wearer (C) subjects. Using a sieving method to study bolus granulometry, percentage of weight of particles retained in different sieves (D) is expressed in terms of size aperture giving particle size distribution curves for bolus from young dentates (green), aged dentates (blue) and aged dentated (red) subjects (n=10). These examples show that aged individuals masticate longer and provide a correct bolus, with similar bolus particle size distribution as obtained for young dentate subjects. On the contrary, despite a longer masticatory sequence, aged denture wearer subjects are not able to form a correct bolus which contains many larger particles (red curve). (modified from Mishellany-Dutour et al 2008, with permission).

3.3 Influence of Food Characteristics on Food Oral Processing and on Food Bolus

Although food oral processing varies according to individual oral capabilities, food structure also plays a prominent role in driving oral functions, especially muscles activity, jaw and tongue movements, which are adjusted to food features as early as the first bite and modulated through the complete masticatory sequence as textural changes occur in the bolus (Lassauzay et al. 2000; Peyron et al. 2002, 2011). Some unclear or insignificant relationships between specific physical dimensions and physiological measurements can be related to a certain complexity in mechanical measurements which cannot be unique for the large variety of foods and applied at different single measurement scale. Nevertheless, the common observation of a dominant link between food and its oral processing remains verified. There is an abundance of literature on how different food characteristics have clearly influenced oral functions (Woda et al. 2006; Rosenthal and Share 2014; Hawthornthwaite et al. 2015; Tonni et al. 2020; Guo 2021). Food oral processing is firstly driven by mechanical fragmentation of food which in turn is largely dependent on food nature and formulation, conferring specific physico-chemical characteristics including geometry (size, water content, volume, shape, weight or initial form), structure, heterogeneity and composition (Aguayo-Mendoza et al. 2019; Guo 2021). These links have been demonstrated for various food families such as bread, meat, dairy products, rice, gels, gums or confectionery (Yven et al. 2005; Jalabert-Malbos et al. 2007; Drago et al. 2011; Le Bleis et al. 2013a; Pentikäinen et al. 2014; Gao et al. 2015; Larsen et al. 2016; Wagoner et al. 2016; Kohyama et al. 2016). Despite some vagueness in mechanically defining various foods, hardness is probably the dominant characteristics used by the central nervous system to control masticatory force. For example, some studies showed that a mechanical index based on toughness and elastic modulus of complex foods can reflect the complex stimulation serving as inputs for the CPG (Agrawal et al. 1997; Lucas et al. 2002).

Indeed, amplitude and duration of muscular contraction during each masticatory cycle (EMG recordings) are related to an increase with food hardness (Horio and Kawamura 1989; Peyron et al. 2002; Kohyama et al. 2003; Foster et al. 2006; Woda et al. 2006). Longer masticatory sequences consequently to higher number of masticatory cycles needed to masticate harder foods have been observed for a wide variety of food families such as rice, meat products, breads, gels or cheeses for example (Figure 7; Aguayo-Mendoza et al. 2019; Pematilleke et al. 2020, 2021; Tonni et al. 2020; Guo 2021). Food recoverability, adhesiveness, springiness or other dimensions measured to characterize food have influence on food oral processing (Kazemeini et al. 2021). Mastication of hard foods also signs for higher and larger jaw displacements, with generally smaller closure angles and higher velocities (Peyron et al. 2002, 2004a; Foster et al. 2006; Piancino et al. 2008). As demonstrated with elastic model foods, amplitude of mandibular movement clearly increases with hardness (Figure 8). These jaw displacements also vary with other physical properties of foods to adapt the right combination of compression and shear constraints to accomplish the optimal mechanical food disruption (Lucas et al. 1986; Agrawal et al. 1997; Foster et al. 2006; Wintergerst et al. 2008). Mastication fibrous products such meat, or more adhesive ones, generally require more shear stresses which is illustrated with more lateral jaw excursion certainly permitting more lateral teeth opposition (Peyron et al. 2002; Foster et al. 2006). As for EMG activities or number of masticatory cycles, amplitude of jaw movement logically increases with food sample size (Peyron et al. 1997; Wintergerst et al. 2008; Goto et al. 2015; Kohyama et al. 2016). An increasing structural heterogeneity of food also results in an increase in food oral processing activity, reflected in a higher number of masticatory cycles, longer mastication duration, or greater muscular activity, for example (Gao et al. 2015; Laguna and Sarkar 2016; van Eck et al. 2019). Dryness is another food characteristic which has been addressed. Saliva impregnation is more important for dry foods, powder products being an extreme in terms of quantity of saliva incorporated in the bolus, harder foods also provoking more saliva production (Mosca and Chen 2017).

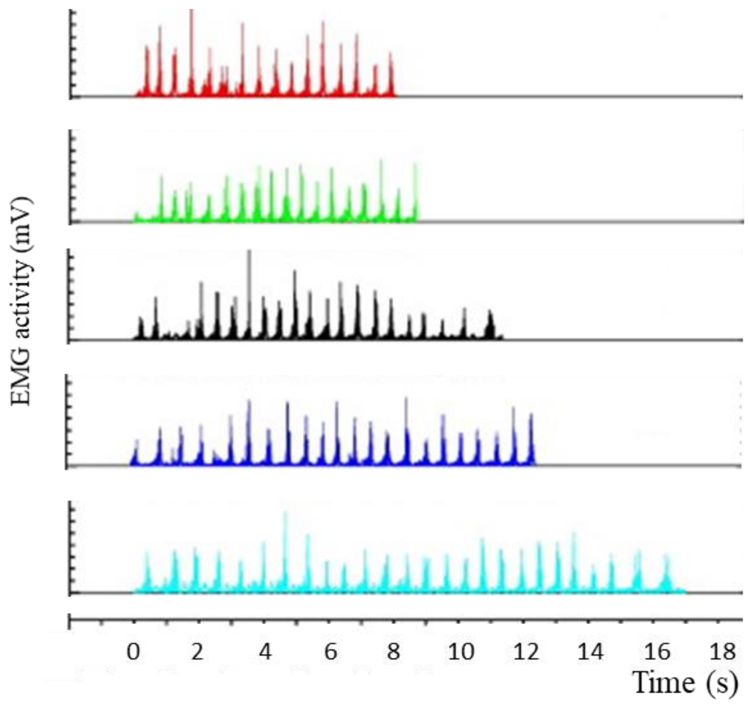
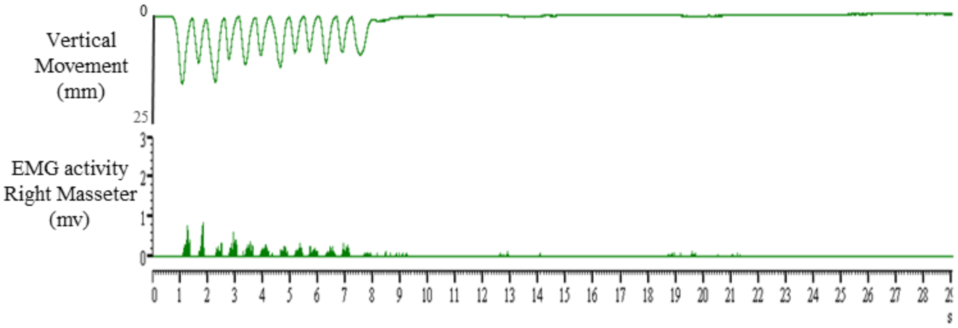


Figure 7: Examples of electromyographic recordings (EMG) obtained for the left temporalis muscle during mastication of 5 different breakfast cereals by the same subject (adapted from Hedjazi et al, 2013; with permission).

Overall and for a wide range of food types, the bolus particle size decreases with the increase in food hardness (Peyron et al. 2004b; Jalabert-Malbos et al. 2007; Chen et al. 2013). As mastication and food bolus formation being dynamic mechanisms, EMG activity as well as amplitude of vertical jaw displacement are gradually reduced with the progress of masticatory sequence, which is attributed both to a regular food softening and decrease in particle size (Lassauzay et al. 2000; Peyron et al. 2002; Grigoriadis et al. 2014). The strongest changes in muscular activity is in amplitude of jaw displacements observed during the first five masticatory cycles, and then decrease more regularly until the end of chewing (Peyron et al. 2002). These changes are proportional to the initial food hardness at the beginning of mastication while less significant at the end when the bolus properties have been reached whatever the initial hardness. Amplitude of tongue movements also increased during management of harder or at least more complex foods (Taniguchi et al. 2013).

In case of semi-solid foods requiring little mastication, the tongue acts as the main tool to break the soft food matrix by squeezing and compressing food against the hard palate. Increasing consistency or resistance to compression of these foods increases tongue activity with increased amplitude of lingual pressure (Kieser et al. 2011; de Wijk et al. 2011; Yokoyama et al. 2014; Nishinari et al. 2020).

A soft elastic model food



B hard elastic model food

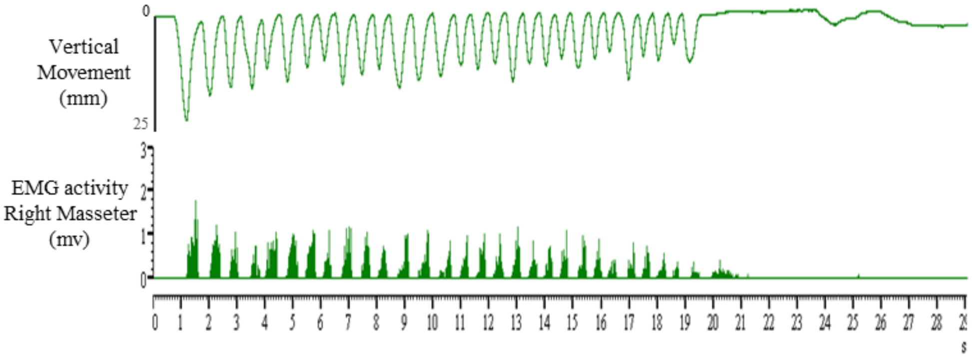


Figure 8: Examples of electromyographic recordings (EMG) obtained from the right masseter in a normo-dentate individual masticating a soft (A) or a hard (B) elastic model food. Amplitude of vertical movement and muscular contraction, number of masticatory cycles significantly increase with hardness.

3.3.1 Swallowing threshold

Transition from mastication to swallowing defines the swallowing threshold. Swallowing is a complex and highly coordinated function which cannot be separated from mastication and which involves tongue, tissues in the oropharynx. The masticatory sequence relates to a dynamic process and a continuous perception of bolus physical properties by receptors in the mouth participate in the central decision of swallowing initiation. The first phase among the three constituting the process swallowing is voluntary and proceed in the oral cavity. It has been initially suggested that it can be triggered when critical particle size, and accurate bolus lubrication, and completed by notion of flow and stretch levels perceived by oral receptors (Lucas and Luke 1986; Hutchings and Lillford 1988; Prinz and Lucas 1995)., the key and common point for swallowing being as effortless as possible whatever the nature of the food. As bolus properties do not reach the correct particle size and lubrication levels to guarantee a safe swallowing, masticatory process continues in a loop model in order to mitigate the risk of swallowing to large particles, not enough salivation incorporation or the risk of their aspiration (Foster et al. 2011; Gray-Stuart et al. 2017). Thus, mechanisms are based on perception of accurate particle size sufficiently lubricated, providing an entity presenting specific rheological features such as plasticity and slipping properties (Prinz and Lucas 1995; Peyron et al. 2011). Several other rheological bolus characteristics have been added in the swallowing threshold description such as flow- and stretch-ability, adhesiveness, plasticity, viscoelasticity and apparent shear viscosity, or cohesive forces allowing particles to cohere each other and form a definable entity, for example (Prinz and Lucas 1997; Chen and Lolivret 2011; Tobin et al. 2020; Pu et al. 2021). Food bolus consistency as well as its volume are also factors generating changes in timing of swallowing steps and in modalities of its propulsion toward pharynx (Chi-Fishman and Stone 1996).

3.4 Challenges and perspectives in food oral processing research area

As an emerging research area in food science discipline, food oral processing study generally depicts mechanisms involved in food texture perception, masticatory effort to form a bolus, saliva action, aroma release and taste perception, bolus and saliva rheological characteristics, etc. Several perspectives have been identified in these research fields and cover comprehensive studies on structure disruption, bolus characteristics at different measurement scales, food-saliva interaction, food oral management, perception, role of tongue, oral digestion, etc, until projections in nutrition.

Plethora literature has reported new research opportunities leading to new front lines of science around interactions between food and mouth. In this dynamic, the most important challenge would be to increase and consolidate physiological considerations in studying oral mechanisms prevailing during mastication and swallowing. Apart production of relevant knowledge, some issues addressed in food oral processing research area can be exploited in designing new foods for specific population such as children, aged and/or orally deficient people. This knowledge is obviously necessary to provide foods of improved textural quality, appropriated to age and individual oral capabilities, healthy and pleasurable, but also matching nutritional requirements.

In this perspective, an important challenge to face is the construction of an efficient and active interaction to join knowledge and work on the interface of physiology, food science and clinical areas, for a relevant and beneficial result for all concerned. Indeed, an important gap still existing is probably an underestimation of physiological concepts in conducting food oral processing research which may lead to undervaluation, incomplete or misinterpretation of results. Simulation of oral processes (mastication swallowing tongue movements and saliva addition…) would also benefit if driven with a good control of physiological concepts governing these functions.

This challenging strategy shall also include caution in choosing methods of measurement, not only for food and food bolus characterisation but also for physiological variables to consider. Saliva-food, saliva-mouth and mouth-food interactions clearly governing mechanisms during food oral processing could certainly be addressed with success if studied at the interface between different disciplines.

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